

EXPERIMENTAL STUDIES OF THE INTERACTIONS BETWEEN A WEB-INVADING SPIDER AND TWO HOST SPECIES

Scott F. Larcher and David H. Wise¹

Department of Biological Sciences
University of Maryland Baltimore County (UMBC)
Catonsville, Maryland 21228

ABSTRACT

Field experiments were conducted to uncover the effects of a web-invading spider, *Argyrodes trigonum* (Hentz), on two spider species that serve as its host, *Neriene radiata* (Walckenaer) and *Metepeira labyrinthea* (Walckenaer). A series of short-term experiments, each lasting one to three days, investigated (1) the effect of host-*Argyrodes* size differentials on the rate of host emigration and mortality, (2) the effect of additional food on host and *Argyrodes* emigration, (3) the rate of immigration to, and emigration from, host-occupied and host-unoccupied webs by *Argyrodes*, and (4) the use of host webs by *Argyrodes*.

The presence of *Argyrodes* resulted in significant host emigration when host-*Argyrodes* weight ratios were below 10:1. In some invasions *Argyrodes* killed the resident spider. Additional prey did not prevent the host from leaving webs containing adult *Argyrodes*, nor did added prey affect *Argyrodes* emigration from webs. *Argyrodes* invaded host-occupied and host-unoccupied webs with equal frequency and captured prey when occupying both types of webs. These latter results suggest that *A. trigonum* may often inhabit and use empty webs for prey capture, as well as webs occupied by the original resident.

Thus, in its interactions with *N. radiata* and *M. labyrinthea*, the web-invading *A. trigonum* behaves perhaps as a commensal, and certainly as a predator, a thief of prey, a web-thief, and perhaps a web-scavenger. The nature of the interaction between *A. trigonum* and its hosts appears to vary primarily as a function of the relative size of host spider and *A. trigonum*.

INTRODUCTION

Spiders of the genus *Argyrodes* are often described as commensals that inhabit the webs of other spiders, consuming prey neglected or undetected by the host [Exline 1945, Archer 1946 (1947), Comstock 1948, Kaston 1978, Gertsch 1979]. Studies of *Argyrodes* spp. have revealed that they also behave as kleptoparasites by stealing prey previously captured by the host [Wiehle 1928, 1931, Thomas 1953, Kullman 1959 (all cited by Kaston 1965); Robinson and Olazarri 1971, Robinson and Robinson 1973]. Kleptoparasitism can be detrimental to the host. Rypstra (1981) showed that prey consumption by the host *Nephila clavipes* (Linnaeus) was significantly reduced with each additional kleptoparasite in the web. Once prey consumption declined below a critical rate, *N. clavipes* abandoned its web site.

¹To whom reprint requests should be addressed.

Argyrodes spp. can also prey on their host. Exline (Exline and Levi 1962) discovered *A. fictilium* (Hentz) eating *Araneus*. Lamore (1958) observed *A. trigonum* (Hentz) eating the basilica spider *Mecynogea lemniscata* (Walckenaer), and Archer [1946 (1947)] reported that *A. fictilium* would kill and eat *Frontinella pyramitela* (Walckenaer). *Argyrodes* spp. have also been found feeding on *Neriene radiata* (Walckenaer) and *Metopeira labyrinthea* Hentz (Wise 1982; J. Martyniuk, pers. comm.). *A. baboquivari* was observed to feed on the eggs, juveniles, and adults of the uloborid *Philoponella oweni* (Chamberlin) [Smith-Trail 1980 (1981)]. In an experimental study, Wise (1982) showed that *A. trigonum* can cause significant mortality in populations of *M. labyrinthea*. He also suggested that web invasions by *Argyrodes* may lead *M. labyrinthea* to abandon their webs. This is consistent with the observation that the webs of *N. radiata* and *M. labyrinthea* are often found containing only *Argyrodes* (pers. ob.).

Argyrodes apparently can behave towards its host as a commensal, a kleptoparasite, or a predator. Responses by the host range from apparent tolerance, through loss of prey, loss of web as a result of emigration, to loss of life. The outcome of a particular interaction between an *Argyrodes* species and its host may be determined by combinations of variables including species and size of the host, species and size of *Argyrodes*, morphology of the host web, food intake of the host and *Argyrodes*, and energy investment by the host and *Argyrodes*. Wise (1982) has suggested that interactions between temperate *Argyrodes* species and their hosts may vary from commensal to predatory as a function of variables such as host feeding rate and relative size of host and *Argyrodes*.

Evidence suggests that the size ratio of host to *Argyrodes* may be particularly important. In situations where the host is very large relative to the web-invading *Argyrodes*, the latter may be incapable of injuring the host, or may risk injury to itself if it attacks the host. In such cases *Argyrodes* may assume the role of commensal or kleptoparasite. Commensal and kleptoparasitic interactions appear to be particularly common between *Argyrodes* and *Argiope* and *Nephila*, hosts which are generally large relative to *Argyrodes* (Robinson and Olazarri 1971, Robinson and Robinson 1973, Vollrath 1979a, Rypstra 1981). When host size approximates that of *Argyrodes*, predation on the host can occur or the host may emigrate soon after *Argyrodes* has invaded its web [Smith-Trail 1980 (1981); Wise 1982].

The level of prey consumption by host or *Argyrodes* may also determine the type of interaction. The host is likely to remain in the web if its food consumption is above a certain level, but will leave the web site if stealing of prey by *Argyrodes* decreases the rate of prey capture below a threshold value (Rypstra 1981). Prey densities might also influence *Argyrodes*' behavior. If the capture rate of small insects by *Argyrodes* is high, it may be less likely to kleptoparasitize or attack its host, particularly if risk to the *Argyrodes* exists.

Invasion of a web by *Argyrodes* may be a quest for a web as well as an opportunity to capture the host. Since *Argyrodes* has been observed in webs without hosts, possibly *Argyrodes* utilizes the web even in the absence of the host. Remaining in the web after the host has emigrated may be beneficial to *Argyrodes* if it can use the empty web to capture prey. The assumed danger of predation while moving to a new web and the complications of finding a suitable host are reduced if more time can be spent in a given web. Apparently to date no one has compared the growth, survival and reproduction of *Argyrodes* in webs with a host to these parameters for *Argyrodes* in vacated webs.

The particular questions addressed by this research are the following: (1) Does comparison of the size of the host relative to that of *Argyrodes* reveal a critical size ratio

where one interaction is more likely than another? (2) Do combinations of particular developmental stages (e.g., adult host with juvenile *Argyrodes*) result in a particular interaction? (3) Does *Argyrodes* of a particular size or developmental stage exhibit different behaviors towards different host species? (4) Does the presence or absence of the host affect the rate of immigration, rate of emigration, and use of the web by *Argyrodes*? (5) Does additional prey affect the rate of host or *Argyrodes* emigration?

Most of the experiments focused on the questions relating to effects of size differences between host and *Argyrodes*. A series of experiments was performed in which a range of host-*Argyrodes* ratios was created. *Argyrodes* of a particular size class were introduced into occupied host webs and observed at three-hour intervals over a 24 hour period. The rate of emigration of those hosts was compared to that of host spiders whose webs were kept free of *Argyrodes*. Two spider species which have only partially coincident life histories (i.e., juveniles and adults of both species do not occur at the same time) were used as hosts so that the behavioral flexibility of *Argyrodes* towards hosts of different developmental stages could be observed.

Experiments to study rates of immigration and emigration involved allowing *Argyrodes* to enter or leave webs with the hosts present or absent over a period of several days. In several experiments of similar design, food was added to some webs and *Argyrodes* movement was compared between supplemented and unsupplemented webs. *Argyrodes* behavior while in host webs was noted; thus, the results of the experiments can be interpreted in the context of specific behaviors of both host and the web-invader.

Argyrodes trigonum (Hentz) (Theridiidae) overwinter as juveniles and are commonly found in antepenultimate or penultimate stages before June. During June and early July mature spiders are present. By late June gravid females and females accompanying egg sacs are abundant. At this time females are sometimes found in small tangles of their own construction as well as webs of other species. In July the spiderlings emerge from the egg sac and early-stage spiders are common. Later-instar *Argyrodes* are commonly found in September, but numbers begin to decline in October.

The life histories of the two host species used in this study, the filmy dome spider *Neriene radiata* (Walckenaer) (Linyphiidae) and the labyrinth spider *Metepeira labyrinthea* (Walckenaer) (Araneidae), contrast with that of *A. trigonum*. Evidence indicates some *N. radiata* complete two generations per year (Wise 1976, in press). Juveniles overwinter and appear in webs in late March or early April. They undergo several molts and reach maturity in May-June. These adults reproduce and spiderlings appear in June-July. Spiderlings that hatched early in the season reach maturity by August or September and produce another generation of overwintering juveniles. Later-emerging spiderlings may overwinter as late-stage juveniles before maturing the next spring. *N. radiata* abundance declines in October and no mature spiders overwinter (Wise 1976). The web of the filmy dome spider is a fine-meshed dome with an extensive tangle above. The spider hangs inverted beneath the center of the dome and captures prey that has entered the tangle by shaking the tangle and pulling the fallen prey through the dome.

Metepeira labyrinthea hatchlings overwinter in the egg sac and emerge in May. Maturity is reached by late July - early August. Females produce egg sacs through October but males disappear in September. The web of *M. labyrinthea* is a composite consisting of a protective tangle and a typical, vertically oriented araneid orb. Within the tangle *M. labyrinthea* builds a protective retreat that often includes web debris or an egg sac. A signal line runs from the center of the orb to the retreat. *M. labyrinthea* generally remains in the retreat and advances to the orb on the signal line to capture prey that has hit the orb.

METHODS

Experiments were conducted in mixed deciduous-pine woods on the Patuxent Wildlife Research Center, Prince Georges Co., Maryland, USA, on natural vegetation and on artificial web sites. The artificial units consisted of a wooden frame 4 m long, 2 m high, and 1.6 m wide. Galvanized wire fencing (5.1 cm mesh chicken wire) composed two 1-meter high rows of undulating waves. These rows were separated by a 1.6 x 4 m horizontal piece of fencing and a similar piece was secured to the top of the unit. The units were distributed approximately 10 m apart on a grid. Host spiders that had colonized or had been introduced onto the artificial web sites were used for the experiments. Spiders on these units were easier to locate and generally easier to remove from their webs than were spiders found on natural vegetation. Removal of spiders found on natural vegetation was difficult because movement of small branches often disturbed the web and webs were often very close to the ground. Webs found on natural vegetation were used when webs located on artificial web sites provided an inadequate sample size. For all experiments 1-8 spiders were added to each of several units. Only 50-60% of these spiders colonized the units, so that at the start of an experiment each unit contained approximately three spiders spaced .5 m to > 3 m apart. For all experiments each web was treated as an individual replicate, since treatments were assigned at random to individual webs, not to units.

Effect of Relative Size of Host and *Argyrodes*.—During the summer of 1982, webs containing adult females or juveniles of the host species were located on the units or, when necessary, on natural vegetation. These spiders were removed from their webs, measured and weighed, then returned to their original locations. These webs were randomized into control (without *Argyrodes*) and experimental (*Argyrodes* added) treatments. *Argyrodes* from host webs on the units or in the surrounding vegetation were then collected, measured, weighed, and introduced into the host webs selected for the experimental treatment.

This type of introduction was conducted several times during the season and encompassed a range of host-*Argyrodes* size combinations: (a) juvenile *Argyrodes* with both juvenile and adult *Neriene* and adult *Metepeira*, and (b) adult *Argyrodes* with juvenile and adult *Neriene* and juvenile *Metepeira* (Tables 1, 2). The different phenologies of *Argyrodes* and the host species prevented all possible permutations from being used.

The number of *Argyrodes* added per web depended upon its size relative to that of the host spider at the time the experiment was conducted. Adult *Argyrodes*, which were always females, were added one to a web for all stages of host spider that were used. Only

Table 1.—Outline of the life history phenologies of the spiders used in this study. The term "spiderlings" is used for animals that have recently emerged from the egg sac. Additional details are found in the text.

	<i>Argyrodes</i>	<i>Neriene</i>	<i>Metepeira</i>
May	Juveniles	Juveniles & Adults	Spiderlings
June	Adults	Adults & Spiderlings	Juveniles
July	Adults & Spiderlings	Juveniles	Juveniles
August	Juveniles	Adults & Juveniles	Adults
September	Juveniles	Adults, Spiderlings & Juveniles	Adults
October	Juveniles	Juveniles	Adults

Table 2.—Stage, average size and weight of spiders in experiments designed to test interactions at different host-*Argyrodes* size ratios. Sample sizes are the number of spiders upon which the means (\pm s.e.) are based. Two numbers beneath sample size represent the number of tibia and weight measurements, respectively, where they are different. Numbers of spiders actually used in the experiments appear in Table 3.

DATE	<i>ARGYRODES</i>						HOST					
	N	STAGE	TIBIA (mm)	WT. (mg)	SPECIES	N	STAGE	TIBIA (mm)	WT. (mg)			
June	8-9	Adult	1.18 \pm 0.03	7.42 \pm 1.02	<i>Neriene</i>	28, 29	Adult	2.32 \pm 0.03	14.38 \pm 0.65			
	15-16	Adult	1.15 \pm 0.02	7.21 \pm 0.02	<i>Neriene</i>	23, 12	Adult	2.38 \pm 0.04	11.83 \pm 0.61			
	27-28	Adult	1.23 \pm 0.02	5.06 \pm 0.35	<i>Metepeira</i>	16	Juvenile	0.61 \pm 0.02	4.28 \pm 0.24			
July	8-9	Adult	1.21 \pm 0.03	5.69 \pm 0.65	<i>Metepeira</i>	38, 37	Juvenile	0.92 \pm 0.03	8.36 \pm 0.63			
	13-14	Adult	1.20 \pm 0.04	5.90 \pm 0.84	<i>Neriene</i>	42	Juvenile	1.61 \pm 0.03	4.86 \pm 0.22			
	25-26	Juvenile	0.29 \pm 0.01	0.29 \pm 0.01	<i>Neriene</i>	65, 66	Adult	2.31 \pm 0.02	12.02 \pm 0.41			
Sept.	6-7	Juvenile	0.47 \pm 0.01	0.79 \pm 0.03	<i>Metepeira</i>	53	Adult	1.55 \pm 0.02	45.05 \pm 2.00			
	18-19	Juvenile	0.51 \pm 0.01	1.10 \pm 0.04	<i>Neriene</i>	50	Juvenile	1.30 \pm 0.03	2.72 \pm 0.13			
	25-26	Juvenile	0.52 \pm 0.01	1.48 \pm 0.04	<i>Metepeira</i>	6	Adult	1.55 \pm 0.06	43.36 \pm 6.18			

one experiment was performed with single juvenile *Argyroides* and an adult host; this experiment, with adult *Neriene* females, demonstrated the difficulty of working with juvenile *Argyroides*. Small *Argyroides* were difficult to manipulate and appeared frequently to move on and off the webs. By introducing more than one juvenile *Argyroides* the probability of having at least one remain in the web was increased. Non-experimental webs often have more than one juvenile *Argyroides* per web. Following the preliminary experiment, three juvenile *Argyroides* were introduced to adult *Neriene* webs to investigate the effect of several small *A. trigonum* on a single mature host. Two juvenile *Argyroides* were added to webs containing mature *Metepeira*. In the *Neriene* - *Argyroides* experiment (September 6-7) that involved juveniles of both species, only one *Argyroides* was introduced per web because of the similarity in size of *Argyroides* and juvenile filmy dome spiders.

Argyroides was added to the support tangle of *Neriene* webs and to the barrier tangle of *Metepeira* webs. Following *Argyroides* introduction each web was censused and the presence or absence and the location of the host or *Argyroides* was noted. Censuses were conducted every three hours for 24 hours. *Argyroides* found in control webs were removed. Adult males of the host species that entered webs were ignored because males visit different female webs and it is difficult to control their presence in the web.

Net Colonization of Host Webs by *Argyroides*.—During September 1981, *Argyroides*' preference for webs with a host versus webs without the host was tested. Sixty-two *Neriene* webs were divided into host-present and host-absent treatments. All *Argyroides* found in the webs were removed. *Argyroides* from the surrounding vegetation were allowed to invade these webs for the following three days, and the number of webs of each treatment that contained *Argyroides* was noted. The preference of *Argyroides* for host-occupied versus host-unoccupied *Metepeira* webs was tested in a similar manner in two separate runs.

In August 1982, the effect of web occupancy by the host on the net colonization by *Argyroides* was tested by direct introduction of *Argyroides*. Fifty *Neriene* webs were marked, and the host spider was removed from 25 webs. Two juvenile *Argyroides* were introduced into all webs. The number of webs containing *A. trigonum* was noted in each of 1-3 censuses conducted each day over the next 72 hours. Two runs of this same experiment were conducted with mature female *Metepeira* and two juvenile *A. trigonum*. Following the first run of the experiment, treatments were reversed so that all webs previously designated as controls had the host removed and the original residents of the removal treatment were returned to their webs.

***Argyroides* Colonization of Food-Supplemented *Neriene* Webs.**—Studies of the effect of food supplementation on the net colonization by mature female *Argyroides* of webs of mature female *Neriene* were conducted with host-unoccupied and host-occupied webs in separate experiments during May and June, 1982.

The use of host-unoccupied webs uncovers the effects of supplemental food on *Argyroides* neglecting any effects due to the host. A single female *Argyroides* was introduced into each of 50 webs from which the host had been removed. Twenty-six of these webs received supplemental prey. Each feeding round involved introducing a termite larva to the tangle and noting whether the *Argyroides* responded to the prey (defined as increased activity when prey was introduced), captured the prey, or did not respond. Termite nymphs, found within rotting logs in nature, are not natural prey of web-building spiders. However, termite nymphs were used because they could be captured easily, remained in the tangle after being introduced, continued to move for long periods of time once in the

tangle, and *A. trigonum* would feed on them. Feeding rounds were performed for three days and a final census was taken on the fourth day. A single feeding round was conducted on day one and two rounds spaced 2.5 hours apart were conducted on day two and three. It was considered that only two feeding rounds were necessary on these days because *Argyrodes* usually were feeding on termites from previous rounds or did not respond to prey introduced in the second round. The experiment was terminated when 50% of the *Argyrodes* had abandoned the web. Data collected included presence/absence of *Argyrodes*, response to the prey, and a subjective evaluation of web quality.

The experiment with host-occupied webs uncovered the effect of supplemented prey on *Argyrodes* colonization with the host present, and also provided additional information on the emigration rate of the host from an *Argyrodes*-occupied web. Before an *Argyrodes* was introduced, a single termite was added to each of 51 webs occupied by a mature female *Neriene*. It was thought this preliminary addition of food might decrease the tendency of *Neriene* to emigrate when an *A. trigonum* was introduced. A mature female *Argyrodes* was added to each web, and prey were added to 26 webs in two feeding rounds spaced two hours apart. Each feeding round consisted of adding two termites to the tangle, separated by a 5-10 min. interval.

By the following day 43 of the hosts had abandoned their webs. *Argyrodes* had also emigrated from six of these webs. The experiment was continued with the 37 webs that contained only *Argyrodes*. Over the next three days 19 of the webs (all from the original food-supplemented treatment) received four termite nymphs. The same data were collected as in the experiment involving host-unoccupied webs.

Behavioral Observations of *Argyrodes*.—Throughout the course of these studies, behaviors of *Argyrodes* and its hosts were noted. These observations include capture of the host spider by *Argyrodes*, the behavior of *Argyrodes* in the web with the host present, kleptoparasitism by *Argyrodes*, and the behavior of *Argyrodes* in a web without a host. These observations will be described in conjunction with the results of the experiments.

RESULTS

Effect of Relative Size of Host and *Argyrodes*.—A significant proportion of adult filmy dome spiders left their webs in response to adult *Argyrodes* (Table 3). Juvenile *Neriene* also abandoned their webs when paired with adult *Argyrodes*, as did smaller *Neriene* in response to juvenile *Argyrodes*. The only *Neriene* - *Argyrodes* combination that did not result in significant host emigration is that in which very small *Argyrodes* were introduced into adult filmy dome webs (Table 3). The additional experiment in which three small *Argyrodes* were introduced to each host web also did not result in significant host emigration ($\chi^2 = 0.004$, $df = 1$, $p > 0.90$; based on emigration of 3/21 control *Neriene* and 3/22 *Neriene* with *A. trigonum*).

Results of the introductions (Table 3) were also analyzed as a 2 x 2 x 5 contingency table in order to determine whether the effect of *Argyrodes* on its host varied significantly as a function of the stages paired. The three-way interaction term is significant ($\chi^2 = 14.19$, $df = 4$, $p = 0.013$), confirming that *Argyrodes* had a varying effect on *Neriene*.

Some combinations of *Argyrodes* and *Neriene* were not studied or observed. Large *Argyrodes* were not usually observed in the webs of extremely small filmy dome spiders, perhaps because their webs are too small to support large *Argyrodes*. Combinations of very small *Argyrodes* and the earliest instar *Neriene* were not studied because of the difficulty of working with first and second instar *Neriene*. Removal of these stages from their webs could not be accomplished without extensive damage to the web.

Table 3.—Results of experiments testing outcome at different host-*Argyroides* size ratios. All probabilities are presented for one-tailed statistics with d.f. = 1. (Rem. = remain; Prop. = proportion).

<i>NERIENE</i>										
Date	STAGE		no <i>ARGYRODES</i>			with <i>ARGYRODES</i>			χ^2	p
	<i>Neriene</i>	<i>Argyroides</i>	N	Rem.	Prop.	N	Rem.	Prop.		
June 8-9	Adult	Adult	27	23	0.85	31	6	0.19	25.02	0.001
June 15-16	Adult	Adult	25	16	0.64	26	7	0.27	7.08	0.005
July 13-14	Juvenile	Adult	14	9	0.64	12	2	0.17	6.00	0.012
July 25-26	Adult	Juvenile	27	22	0.82	30	25	0.83	0.04	N.S.
Sept 18-19	Juvenile	Juvenile	25	16	0.64	23	4	0.17	10.71	0.002

<i>METEPEIRA</i>										
Date	STAGE		no <i>ARGYRODES</i>			with <i>ARGYRODES</i>			χ^2	p
	<i>Metepeira</i>	<i>Argyroides</i>	N	Rem.	Prop.	N	Rem.	Prop.		
June 27-28	Juvenile	Adult	21	19	0.90	21	3	0.14	24.44	0.001
July 8-9	Juvenile	Adult	19	16	0.84	18	1	0.06	23.03	0.001
Sept 6-7	Adult	Juvenile	24	24	1.00	24	24	1.00	0.0	N.S.
Sept 25-26	Adult	Juvenile	25	25	1.00	25	24	0.96	1.02	N.S.

Adult *Argyroides* increased the emigration rate of juvenile *Metepeira* (Table 3). Small and intermediate-sized juvenile *Argyroides* had no effect on adult *Metepeira* emigration. It should be noted that in the latter experiments two small *Argyroides* were introduced into the webs because it was assumed *a priori*, based on the previous results obtained from adding single *Argyroides* to mature *Neriene* webs, that single small *Argyroides* would not affect adult *Metepeira*. The differential response of *Metepeira*, which varied with the relative size of host and *Argyroides*, was statistically significant (χ^2 of three-way interaction term from 2 x 2 x 4 table = 10.48, df = 3, p = 0.03). The relative size of the host and invading *Argyroides* was quantified by calculating the weight ratio of host to *Argyroides*. Low ratios correspond to a high emigration rate for both host species (Fig. 1).

Certain size combinations of these species do not occur. Adult *Argyroides* do not coincide with adult *Metepeira*. There may be some overlap between very small *A. trigonum* and large juvenile *Metepeira*, but these combinations were not studied because *Metepeira* populations were lower during 1982 than previous years (unpubl. data) and we were unable to locate enough host spiders for an adequate sample size.

Predation on the host spider was observed only early in the season, when mature *Argyroides* were introduced to the host webs containing mature *Neriene* or juvenile *Metepeira* (Fig. 2). *Argyroides* that were feeding on a host spider at the first census the predation was observed were still feeding on the host at the next census 93% (12/14) of the time. Therefore it appears that most required a minimum of three hours to complete feeding on a captured host. Because webs were censused every three hours, it is reasonable to assume that predation by *Argyroides* was rarely mistaken for emigration of the host. Possibly a captured host may have been discarded or lost for some reason before the capture had been recorded, but this seems to have been an infrequent event.

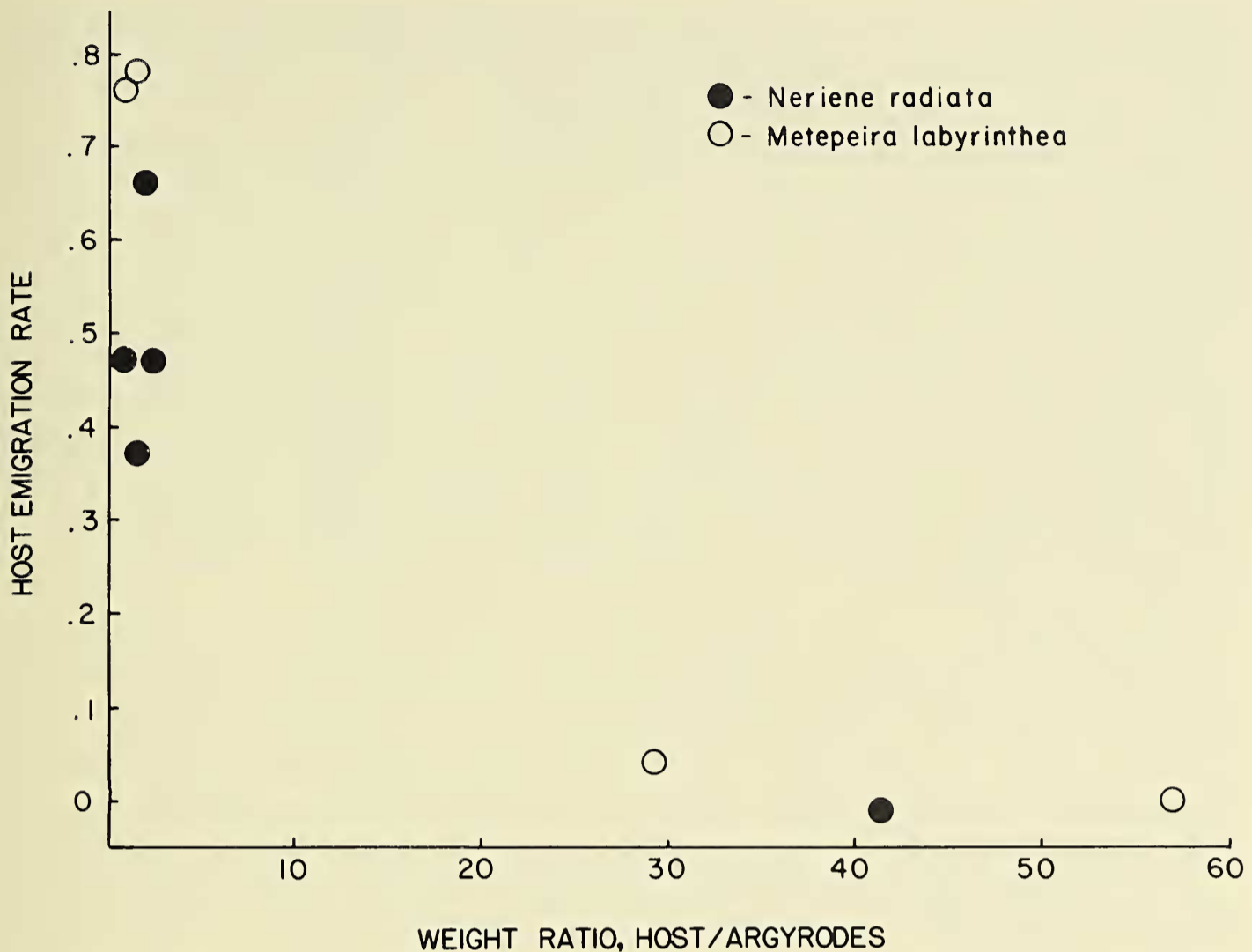


Fig. 1.—The effect of increasing host-to-*Argyroides* weight ratio on host emigration. Host emigration due to the presence of *Argyroides* was estimated by subtracting emigration rate in the control from that in the experimental treatment.

Net Colonization of Host Webs by *Argyroides*.—Two experiments conducted in 1981 indicate that web invasion by *Argyroides* is not affected by the presence of the host. *Argyroides* were allowed to invade host-occupied and host-unoccupied *Neriene* or *Metepeira* webs. *Argyroides* invaded 48% (15/31) of the occupied and 39% (12/31) of the unoccupied *Neriene* webs ($\chi^2 = 0.59$, $df = 1$, $p > 0.25$; 2 x 2 contingency table). Pooled data for two runs of the same experiment using *Metepeira* hosts reveals that 35% (13/37) of host-occupied webs and 43% (16/37) of host-unoccupied webs were invaded by *A. trigonum*. As with the *Neriene* experiment, there is no statistically significant difference between invasion rates of each type of web by *Argyroides* ($\chi^2 = 0.51$, $df = 1$, $p > 0.25$).

Argyroides that were introduced into host webs during the experiments investigating the effects of relative size of host and *Argyroides* on host emigration did not necessarily remain in the web (Fig. 3). The proportion of *Argyroides* that abandoned the experimental webs appears relatively constant for *Neriene* but somewhat erratic for *Metepeira*. It was hypothesized that *Argyroides* would be more likely to abandon the host web when the host is relatively large and *Argyroides* has no effect on host emigration. Two juvenile *Argyroides* were introduced to each of 25 host-occupied and 25 host-unoccupied *Neriene* webs. These *Argyroides* were allowed to emigrate from the webs for approximately 72 hours. Presence of the host had no significant impact on the emigration rate of *Argyroides*. Four left from 25 occupied webs, and none left the empty *Neriene* webs ($p = 0.11$, $df = 1$; Fisher's Exact Probability Test). Two runs of a similar experiment with *Metepeira* webs yielded similar results, though overall emigration rates were higher. Data for these runs were pooled because there was no discernible difference between the size of *Argyroides* or size of *Metepeira* used in each run. Thirty-six percent (17/47) of the *Argyroides*

left the *Metepeira*-occupied webs whereas 22% (11/50) left the host-unoccupied webs. There is no indication of a preference by *Argyrodes* for either occupied or vacant webs ($\chi^2 = 2.40$, $df = 1$, $p > 0.10$; 2 x 2 contingency table).

***Argyrodes* Colonization of Food-Supplemented *Neriene* Webs.**—*Argyrodes* placed in webs from which the host had been removed did not differentially abandon webs in response to food supplementation (Fig. 4a; $\chi^2 = 0.002$, $df = 1$, $p > 0.90$; 2 x 2 contingency table). When food was introduced into webs containing mature *Argyrodes* and mature *Neriene*, web abandonment by *Neriene* over the next 24 hours was high and did not differ between treatments (Fig. 4b; $\chi^2 = 0.004$, $df = 1$, $p > 0.90$). In the same time period few *Argyrodes* left the webs, and their rate of emigration did not differ between food treatments (Fig. 4c; $\chi^2 = 0.60$, $df = 1$, $p > 0.25$). Feeding rounds were continued using webs that contained only *Argyrodes*. Their disappearance was analyzed between treatments. Following six feeding rounds (3 days), rates of web abandonment by *Argyrodes* did not differ between experimentals and controls (Fig. 4d; $\chi^2 = 0.249$, $df = 1$, $p > 0.50$).

Observations of *Argyrodes* Behavior in Host Webs.—(1) Occupation of Web Space by *Argyrodes*. *Argyrodes* that occupy an abandoned *Neriene* web are often found in the dome in the location previously occupied by the host. A sample of 52 webs derived from the seventh or eighth census of the host-*Argyrodes* relative-size experiments that contained only *Argyrodes* revealed that in 75% (39/52) of the webs, *Argyrodes* was in the dome. *Argyrodes* was in the dome in only 35% (6/17) of the webs that contained the host. *Argyrodes* always occupied the barrier tangle of *Metepeira* webs, regardless of host presence (based on 36 host-occupied and 15 host-unoccupied webs).

(2) Prey Capture by *Argyrodes* in Host-Unoccupied Webs. *Argyrodes* captured introduced prey when occupying a web abandoned by the host. Termites were introduced into 41 *Neriene* webs containing only *Argyrodes*. Fifty-four percent (22/41) captured the

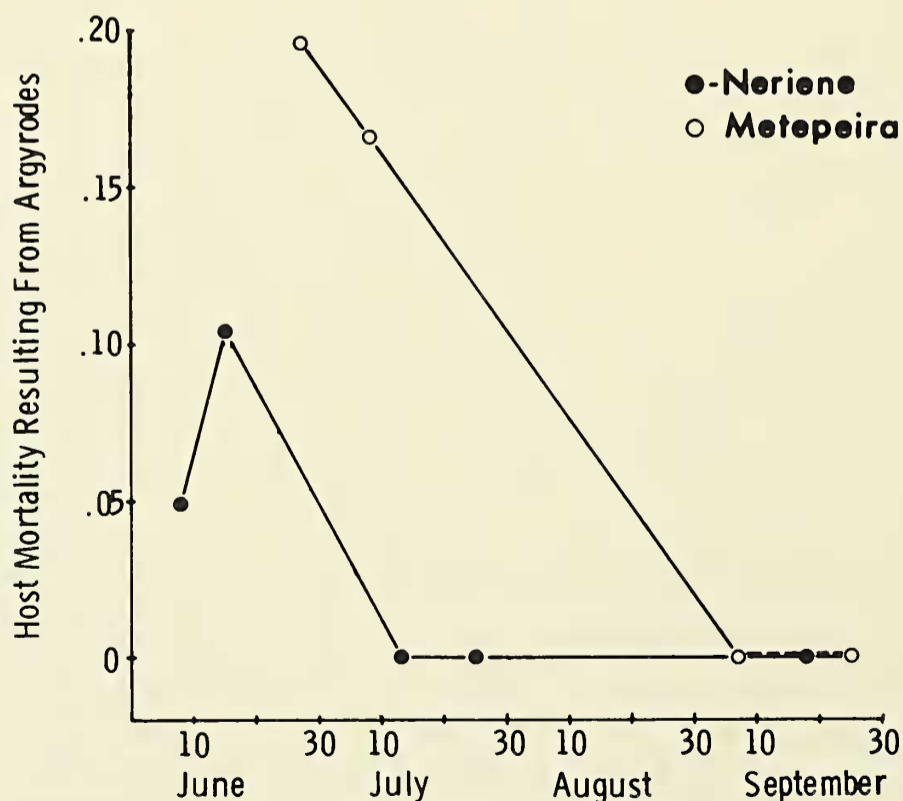


Fig. 2.—Host mortality resulting from *Argyrodes*. Data are derived from the experimental treatments of host-*Argyrodes* relative size experiments.

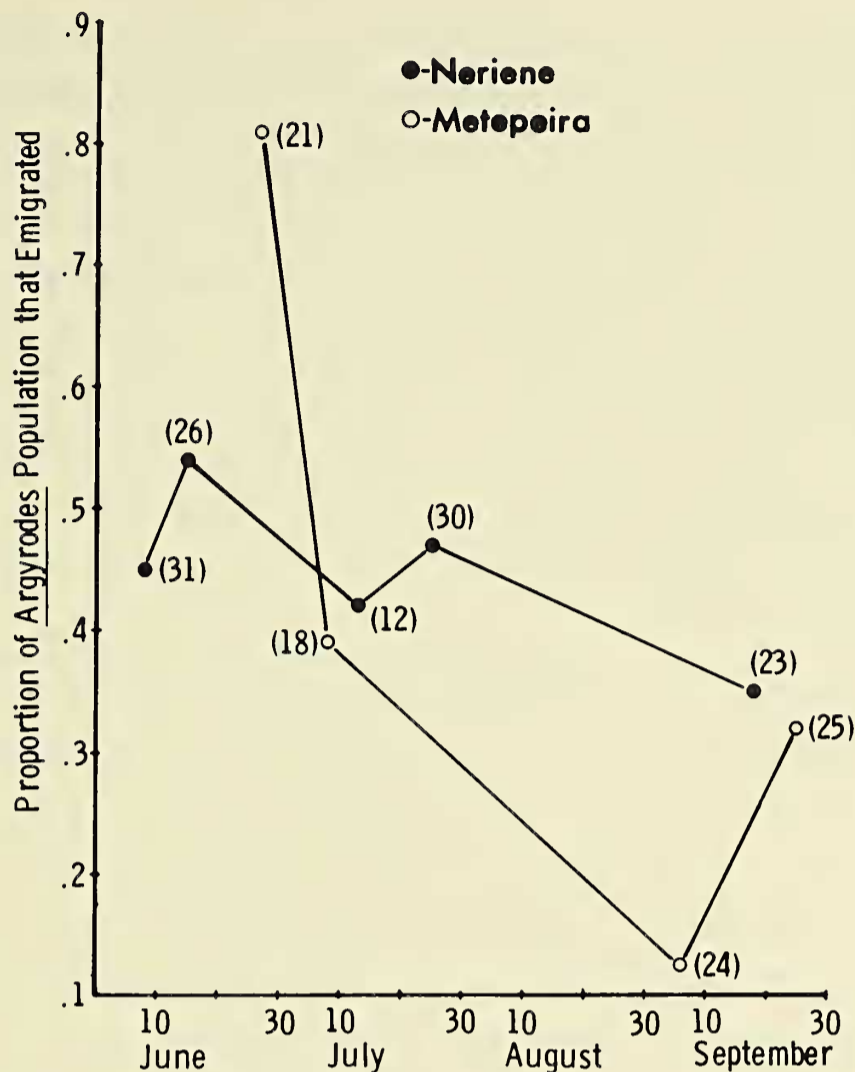


Fig. 3.—Emigration of *Argyrodes* from host webs during host-*Argyrodes* relative size experiments. Sample size is in parentheses.

prey. These data agree with a preliminary experiment in which *Drosophila* were introduced to *Argyrodes*-occupied *Neriene* webs. Fifty-three percent (9/17) of the *Drosophila* was captured by the *Argyrodes*.

Argyrodes that occupy webs containing the host appear to be aware of host movements. During June 1981 *Argyrodes* were introduced into host-occupied webs and observed for periods up to one hour. *Argyrodes* responded to movement in the dome by outstretching their legs and rotating one leg of the first pair in an apparently searching manner. *Argyrodes* sometimes moved towards the host when the host was wrapping prey and moved away if approached by the host. On one occasion the *Argyrodes* dropped to a lower portion of the web when chased by the host *Neriene*. In another instance a labyrinth spider approached the *Argyrodes*, made contact with the invader, and retreated across the web while being followed by *Argyrodes*. Observations of host-*Argyrodes* combinations throughout this study produced several generalizations: (a) *Argyrodes* movement in the tangle or dome of the *Neriene* web or near the retreat of the *Metepeira* web caused the host to stop its own movement or to retreat from the area of the *Argyrodes*, and (b) all host spiders that moved away from an *Argyrodes* later abandoned their webs.

Two observations of kleptoparasitism by mature *Argyrodes* were noted. In the first example the host *Neriene* was wrapping a prey item in the dome. The *A. trigonum* moved into the dome and approached within 3 cm of the host and prey. The *Argyrodes* was

chased by the host and dropped to a lower portion of the dome. The host retreated to the opposite side of the dome, leaving the wrapped prey in the upper portion of the dome. The *Argyrodes* returned to the prey and began to wrap and feed on the prey. The *Neriene* did not return to the upper dome and later abandoned the web. In the second example an *Argyrodes* was in the tangle above a *Metepeira* retreat. The host was in the retreat feeding on a coleopteran. The *Argyrodes* approached the tent and touched the beetle. The host immediately left the retreat and web. The *Argyrodes* began to feed on the abandoned prey. In both of these examples the host made no attempt to reclaim the prey and, instead, retreated from the web once it was aware of *Argyrodes*' presence.

(3) Capture of the Host by *Argyrodes*. Mature *Argyrodes* were commonly found feeding on females and males of the host species. We never observed the actual capture of a *Neriene* female, but have witnessed the capture of a male *Neriene* and a juvenile *Metepeira* by a mature *A. trigonum*.

An *Argyrodes* was in the dome of a *Neriene* web, with the displaced female in the lower portion of the dome. A *Neriene* male entered the web and was approached and touched by the *Argyrodes*. The male did not retreat and the *Argyrodes* bit the first right leg. This leg was then wrapped with silk and the *Argyrodes* bit the third right leg. All right legs were wrapped and then the entire spider was wrapped. Approximately 30 minutes later the *Argyrodes* began to feed on the dead *Neriene*.

In the other instance an *Argyrodes* was introduced into a web containing a juvenile *Metepeira* that was wrapping a prey in its retreat. The labyrinth spider appeared aware of the *Argyrodes* but did not retreat as the *Argyrodes* approached it by climbing the signal line that runs from the orb to retreat. The *Argyrodes* bit the *Metepeira*, which appeared to die within a minute.

In both cases of an observed capture of a host species by *Argyrodes*, wrapping of the prey was not observed until after a bite had occurred. This differs from situations in which *Argyrodes* catches small insect prey by using a wrap-bite behavioral sequence. An observation of a very small *Argyrodes* attempting to capture a large host indicates that the bite-wrap sequence might regularly be employed when *Argyrodes* is attempting to capture large prey. A small *A. trigonum* was observed to approach an adult *Neriene* and bite its fourth leg. The *Argyrodes* made no obvious attempt to restrain the host and no obvious damage to the host resulted from the attack.

DISCUSSION

Argyrodes trigonum causes web abandonment by *Neriene* throughout a large portion of the season that these spiders occur together. The only combination that does not result in significant host emigration (juvenile *Argyrodes* and adult *Neriene*) represents a period of 3-4 weeks. Significant impact of *Argyrodes* on *Metepeira* occurs in June and July (adult *Argyrodes* and juvenile *Metepeira*) but not in September when *Argyrodes* are very small relative to the adult *Metepeira*. One can tentatively predict that weight ratios of host to *Argyrodes* below approximately 10:1 will result in significant host emigration. This value is only an approximation, since some host-*Argyrodes* ratios were not studied. Unfortunately, *M. labyrinthea* populations were low during 1982, and no data for combinations common during late July and August were collected. Consequently, it is unknown if there is a transition in *Argyrodes*' impact as juvenile *Argyrodes* enter the webs of late-stage *Metepeira* juveniles. A prediction could be made that *Argyrodes* would have little effect on larger juvenile *Metepeira* if the weight ratio of host-to-invader is greater than 10:1.

Apparently the critical weight ratio of approximately 10:1 is similar between host species, which suggests that weight ratios might be applied as a predictor of the outcome of host-*Argyrod*es interactions. Previous studies have shown that spiders monitor vibrations in the web to locate the position of other organisms (Witt 1975, Suter 1978, Vollrath 1979b). Weight is an indicator of size; and if the host is large enough, *Argyrod*es may not attempt to oust the host because of the threat of injury. Studies have shown that weight is an important determinant of outcome in intraspecific contests for web occupancy for an agelenid (Riechert 1978) and the labyrinth spider (Wise 1983). Predation by the conspecific appears to be relatively rare for these species. If, as these studies indicate, the heavier spider frequently gains control of the web site, then one might expect *Argyrod*es to rarely displace the host since *Argyrod*es is usually the smaller of the two. However, *Argyrod*es *trigonum* clearly has evolved the specialized behavior of preying upon the original occupant of the web, which no doubt explains the readiness of large residents to vacate their webs when invaded by *Argyrod*es.

In situations where a single *A. trigonum* does not force the host from the web, it was found that several small *Argyrod*es also did not cause host emigration. The total weight of several small *Argyrod*es does not reach the critical ratio that might lead to host abandonment. Also, these small *Argyrod*es do not seem capable of injuring the host. It is rare to see more than three *Argyrod*es in either *Metepeira* or *Neriene* webs.

Fewer than 20% of the adult *Neriene* were captured by introduced adult *Argyrod*es. No juvenile *Argyrod*es was found with a captured *N. radiata*, and no juvenile *Neriene* was found dead with any stage of *Argyrod*es. Perhaps juvenile *Neriene* are more likely to abandon their web than mature females because juveniles are smaller and more vulnerable to predators such as *Argyrod*es. Since only 4.9% (6/122) of all *Neriene* were captured by *Argyrod*es in the five experiments investigating the role of size differences, it appears that *Argyrod*es is not an important direct source of *Neriene* mortality. *Argyrod*es may, however, be a source of indirect mortality, since displaced *Neriene* may suffer higher mortality from a variety of sources while off the web.

Metepeira were also not often captured by *Argyrod*es. Only adult *Argyrod*es were observed capturing juvenile *Metepeira*. The overall rate of successful attacks by *Argyrod*es on *Metepeira* was approximately 8.0% (7/88). Thus it appears mortality rates from *Argyrod*es may be of similar importance for *Metepeira* and *Neriene*. These rates for both host species measure the outcome of introduced interactions, and are most valuable for comparing interactions between different size classes. These measured mortality rates provide no direct indication of the role or importance of *Argyrod*es mortality in the population dynamics of the filmy dome and labyrinth spiders. These experiments give no indication of how frequently a host spider is exposed to *Argyrod*es invasions during its life, nor do they indicate whether mortality from *Argyrod*es web invasions, either direct or indirect, is density-dependent.

Predation by *Argyrod*es cannot necessarily be assumed when an *Argyrod*es is found feeding on a dead host spider, particularly when the host spider is over 10x the size of the *Argyrod*es. A demonstration in which 15 dead *N. radiata* were introduced into the tangle of webs containing only *Argyrod*es resulted in three of these dead spiders being eaten by *A. trigonum* within three hours of introduction. This is evidence that *Argyrod*es will scavenge dead prey; thus, observations of juveniles feeding on host spiders should not be unexpected. For instance, towards the end of the season, *Metepeira* reaching the end of

their life are often found dead in their webs. If the web is inhabited by juvenile *A. trigonum* at the time of the host's death, it would not be unlikely to find the *Argyrodes* feeding on the dead host.

Argyrodes occupying *Neriene* webs abandoned by the host are often found in the dome as well as the tangle. From either of these locations *Argyrodes* can successfully capture prey that enters the web. *Argyrodes* do not appear to differentially abandon webs with or without hosts. This suggests that *Argyrodes* can benefit from a host web regardless of presence or absence of the host, and that the multiple benefits of a potential meal or a web for catching prey are available to the *Argyrodes*. Rates of immigration of *Argyrodes* into host-occupied and host-unoccupied webs do not differ for both the filmy dome and labyrinth spiders. This suggests that the presence of the host is not the principal attraction to the *Argyrodes*. If host presence was important in terms of being a potential food source, or as a source of prey capture for the kleptoparasite, the net colonization of *Argyrodes* should have been higher in host-occupied webs. The primary factor limiting the use of the web by *Argyrodes* appears to be the web's structural integrity. The *Neriene* web is not particularly sturdy and *Argyrodes* do not appear to substantially reinforce the structure. *Argyrodes* has been observed to strengthen the tangle of a *Metepeira* web with additional silk. This silk could serve the dual functions of additional support or creating denser mesh for increased capture efficiency.

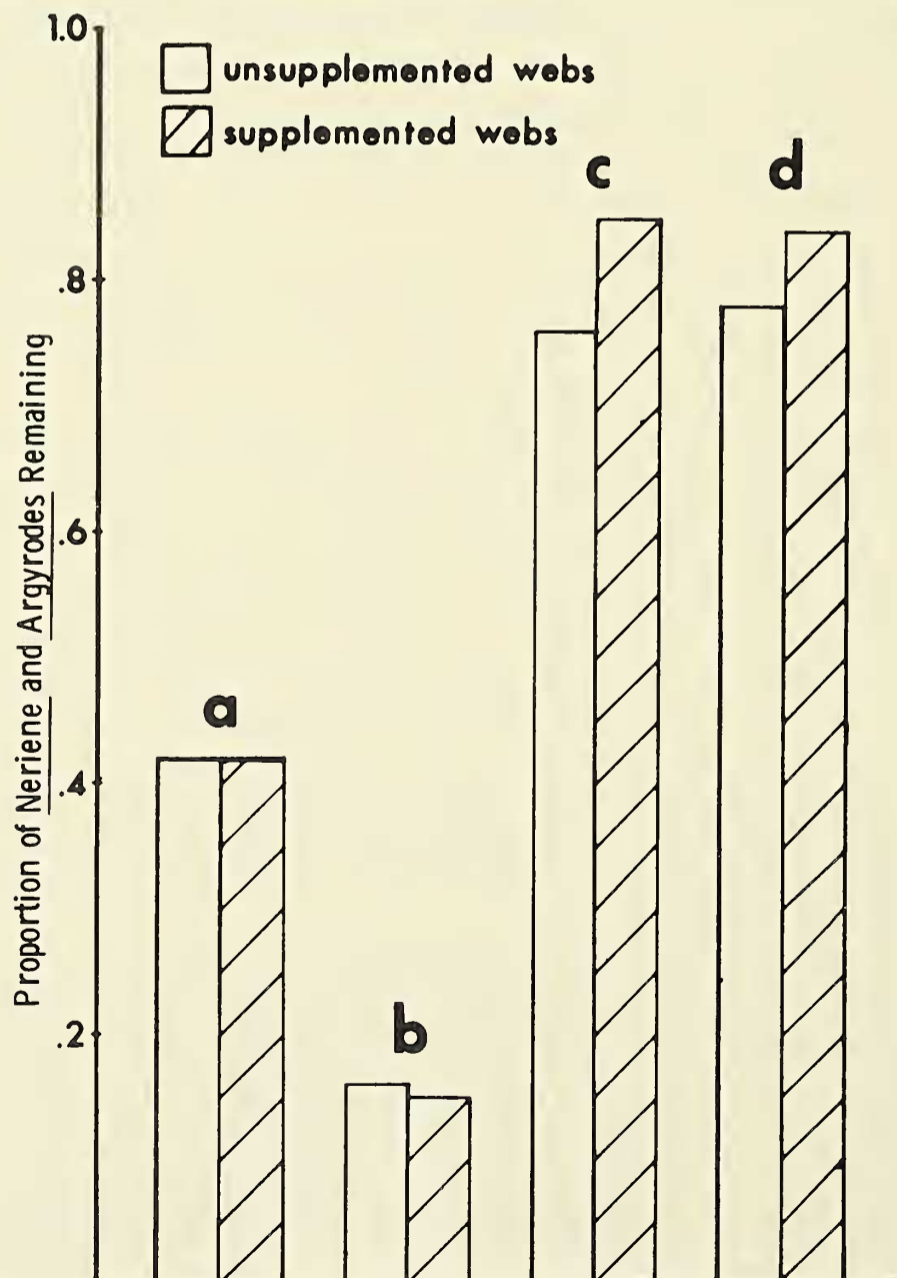


Fig. 4.—Effect of food supplementation on proportion of *Neriene* and *Argyrodes* remaining in the web. Details appear in the text.

Food supplementation did not improve the probability that a mature *Neriene* would remain in a web occupied by a mature *Argyrodes*, nor did supplemental prey increase the probability of *Argyrodes* remaining in the web, whether occupied by the host or not. This suggests that additional food will not influence *Neriene* to risk staying in the web with *Argyrodes*, nor will additional food influence emigration of *Argyrodes*. Because of the limited number of such experiments in this study, interpretations must remain tentative. Prey may not have been in short supply in 1982 for *Neriene* or *Argyrodes*. However, lack of an effect of added prey on the tendency of *Neriene* to vacate the web more likely reflects the fact that *Argyrodes*' major potential impact upon the adult filmy dome spiders is that of a predator, not a prey kleptoparasite. Added prey may not have reduced the emigration rate of *Argyrodes* because it does not repair the empty filmy dome web, and thus web-site quality is more a function of web integrity than short-term prey capture rates. These questions require further study.

Prey kleptoparasitism may play a minor role in *Neriene-Argyrodes* interactions, since the filmy dome spider abandons its web when all but the smallest *Argyrodes* enter the web. Kleptoparasitism may play a more important role for *Argyrodes* that inhabit the webs of mature labyrinth spiders, since this host and invader coexist in the web for the latter 2-3 months of the season (Aug.-Oct.). During periods when *Argyrodes* and its hosts coexist in the web, there is no indication that prey stealing by *Argyrodes* leads to the increased web abandonment that was found in the *Nephila-Argyrodes* system studied by Rypstra (1981). If one defines commensalism in terms of the net fitness of both species, then possibly the cohabitation of small *Argyrodes* and either host is a commensal relationship, since there is no apparent damage to the host spiders. Longer-term experiments are needed, however, to establish conclusively that the presence of even small *Argyrodes* does not lower the fitness of the host. Parameters such as net fecundity of the host with and without the presence of *A. trigonum* should be studied before all possibilities of detrimental effects to the host resulting from *Argyrodes* presence are ruled out.

The term "kleptoparasitism" is usually used to describe a specialized type of competitive behavior, in which one species steals another's prey. The theft of the host's web by *Argyrodes* can be viewed as an example of web kleptoparasitism. This behavior of *Argyrodes* fulfills the definition of kleptoparasitism for several reasons. First, the loss of the web represents an energetic loss to the original owner, since it must build a new web, using energy that could have been applied to future growth or egg production. Also, the act of moving to a new web site may increase the probability of being preyed upon. Either result would reduce fitness. Secondly, the theft of the web represents an energetic gain by the thief. *Argyrodes* captures prey in the stolen web, and on occasion produces an egg sac in the web. *Argyrodes* will inhabit the dome of the *Neriene* web as did the host or will reinforce the tangle of the *Metepeira* web, thereby possibly increasing the web's capture efficiency. Habitation of the web may also improve *Argyrodes*' chances against predators during times when it is not feeding. These points suggest that the net fitness of *A. trigonum* is improved when inhabiting a web abandoned by its host. Further evidence that *Argyrodes* views the web of other species as a resource is the fact that *Argyrodes* are equally attracted to webs with and without hosts. Finally, this specialized behavior towards other species is a one-way competitive interaction—*Argyrodes* does not build a web for other species to capture. Hence the specialized term of "web kleptoparasitism" appears appropriate.

Argyrodes may experience disadvantages to inhabiting an empty web. If the host were to remain and continue normal web maintenance in the presence of *Argyrodes*, the

amount of time that *Argyrodes* could remain at the web site should increase, since apparently *Argyrodes* does not have the ability to spin the variety of webs spun by the species it parasitizes. Also, *Argyrodes* might conserve energy by not being required to perform web maintenance. However, these disadvantages may be outweighed by gains accrued by not behaving as a commensal. The energy provided to the *Argyrodes* by the capture of the host may be more than the energy conserved by continued presence of the host in the web. Also, kleptoparasitism of prey may not be more efficient than capturing live prey, particularly since possible risk of capture by the host exists.

The lifestyle of *Argyrodes* is characterized by an ability to generalize its behavior when invading the webs of different host species. *Argyrodes*' flexible behavior makes possible the exploitation of different species with nonsynchronous phenologies. Assuming *Argyrodes* moves from web to web in a largely random manner, the species of potential host next encountered should primarily be a function of that species' relative frequency in the habitat. *Argyrodes*' quest for a habitable web is made more successful by not having to search for a single host species, or a particular size class of host.

A. trigonum possibly is a commensal, and certainly behaves as a prey kleptoparasite and host-predator. Which alternative behavior *A. trigonum* exhibits appears to depend primarily upon its stage of development and the size of the host spider. Our research suggests that, in addition to exhibiting these behaviors, *A. trigonum* spends considerable time searching out the web of its host species, independently of whether or not the host spider is present. We propose that *A. trigonum* and possibly other *Argyrodes* spp., behave as web kleptoparasites in addition to being web commensals, prey kleptoparasites, and predators on their hosts.

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